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OBSERVATIONS ON THE MASS MIGRATION OF DESERT LOCUST HOPPERS

By John S. Kennedy, Ph.D.

(*Late Locust Officer, Middle East Anti-Locust Unit.*)

Manuscript received 16 October, 1944.

(Read 27 April, 1945.)

With One Text-figure.

The following observations were made on hopper bands of *Schistocerca gregaria* Forskål of the gregarious phase in Persia and Kenya in 1943–44. Attention was concentrated on the analysis of the factors controlling the direction of march. The diurnal activity regime of these hoppers is fairly well understood, but the extensive literature on marching directions is full of apparent anomalies and offers few guiding principles. It was hoped that any regularity detected might help in the more difficult study of migration by flying swarms.

II. General Description.

The bulk of the observations were made in June, 1943, in a few valleys to the south of Kerman, Persia. The country is mountainous and semi-desert with patches of intensive, irrigated cultivation in rich variety in and around the walled villages in the valleys. The first general impression was of numerous separate bands descending from the foot-hills and converging into the fields and gardens of the villages. This first impression was mistaken, as is often the case, for there had been little hatching in the hills to the south and the main movement was therefore from the north. Records of directions being followed by individual bands confirmed a southward trend on open ground (Table 1). On the other, northern, side of the same mountain mass (Kuh-i-Gudar), the bands were said to have descended into the villages from the foot-hills in the same way, moving generally northwards in this case.

In the former area, extending between Bahramjird and Rayin, where these observations were made, the southward trend was in varying degrees lost by bands that encountered broken ground. In the face of a simple obstacle, like a water channel, there would be only a simple deviation of the hoppers' path. Inside a village with its buildings, walls, irrigation channels, trees, etc., bands broke up into a multitude of separate streams moving in all directions. There was no evidence of distant convergence on a village from a variety of directions. The gathering of hoppers into villages and their adjacent fields seemed to be due merely to the cessation there of sustained marching in one direction. Infested villages slowly cleared again as successive detachments of hoppers happened to reach the outskirts where straightforward movement supervened once more.

Parallel movement by a number of separate bands at the same time was clearly evident (*e.g.*, Nos. 10–13 and 15–18, Table 1), although even on open ground exceptions could be found. Only a few opportunities occurred for observing day-after-day behaviour of single bands. One band (Nos. 2–3) resumed marching one morning in the same southward direction as on the previous evening. Another band (Nos. 13–15 and 19–20) continued to move south both morning and afternoon for three days at least. Another (Nos. 21

and 24) was seen moving north one evening and north again three evenings later, while two further bands (Nos. 6–9) moved north both morning and afternoon. The morning and afternoon marching periods were nearly enough of equal duration for one to assume no reversal as a rule, in view of the general southward trend.

The hopper bands on the southern shores of Lake Naivasha, Kenya, in May, 1944, were less closely observed, but certainly presented a less orderly picture

TABLE 1.

Marching directions in relation to sun and wind, recorded when marching was general and not apparently affected by local features.

Obs. No.	Hopper instars	Date	Time (local)	Place	Approx. deviation of marching direction (in degrees)			Remarks
					From due N.	From due up-sun	From due down-wind	
1	I–III	4.vi.43	0900	Gulumak	0	270	No wind	Large
2	,,	,,	1750	Ahmadabad	190	260	,,	Another large
3	,,	5.vi.43	0830	,,	200	100	?	Same as 2
4	,,	,,	1610	Shahabad	10	90	220	Large
5	I–II	18.vi.43	1630	Kerimabad	190	270	Var. wind	Large
6	,,	22.vi.43	a.m.	Gudar	340	245	180	Large
7	IV	,,	,,	,,	340	245	180	Another
8	,,	,,	p.m.	,,	340	65	180	Same as 6
9	,,	,,	,,	,,	340	65	180	Same as 7
10	I–II	23.vi.43	0800	,,	190	105	?	Another
11	,,	,,	0810	,,	180	95	?	Another
12	,,	,,	0850	Gulumak	180	90	?	Small
13	III–IV	,,	0900	Bahramjird	170	75	?	Large
14	,,	,,	1530	,,	180	270	No wind	Same as 13
15	,,	24.vi.43	0820	,,	170	85	?	Same as 14
16	,,	,,	0900	Daulatabad	170	75	?	Another large
17	,,	,,	1015	Husainabad	170	65	?	Very small
18	,,	,,	1040	Gudar	180	70	?	Another do.
19	,,	,,	1750	Bahramjird	200	270	20	Same as 15
20	,,	25.vi.43	0900	,,	205	110	Var. wind	Same as 19
21	IV–V	29.vi.43	1700	,,	350	70	?	Another small
22	,,	,,	,,	Husainabad	140	220	?	Large
23	,,	,,	,,	Daulatabad	45	125	?	Another large
24	,,	2.vii.43	1800	Bahramjird	40	105	20	Same as 21
25	V	16.vii.43	1030	Nishapur	40	285	220	Large
26	I–II	10.v.44	0930	L. Naivasha	360	80	0	Large
27	,,	,,	1030	,,	70	20	80	Same as 26 after overcast period
28	,,	12.v.44	1000	,,	150	90	0	Small
29	,,	,,	,,	,,	150	90	0	Another do.
30	,,	,,	,,	,,	150	90	0	Another do.
31	,,	,,	1030	,,	45	0	255	28 and 29 fused
32	,,	,,	,,	,,	135	90	10	Same as 30
33	,,	15.v.44	0830	,,	10	290	0	Another do.
34	I–III	20.v.44	1715	,,	270	0	270	Another do.

Nos. 1–24 in district south of Kerman, Persia; No. 25 in North Persia; Nos. 26–34 in Kenya Highlands.

than those in Persia. There was no general trend in one direction or another among the numerous bands at the same time, or over a period. Three separate bands (Nos. 28–30) marched in parallel for a short time one morning, but later two of them changed direction and merged into one. The vegetation cover is much denser than in Persia, and the countryside much more cut up by agricultural development, with few uninterrupted expanses of open ground. Sunshine was intermittent, not continuous as in Persia.

It may be useful here to describe the behaviour of a band of Ist–IIIrd stage hoppers observed on the morning of 4th June 1943 in the Kerman district. The behaviour of this band presented great variety within a small area, behaviour quite typical of the effects of a number of natural features, and will thus serve as an introduction to the separate consideration of the influence of particular

features. It was watched for about 2½ hours between 8 and 11 a.m. (Local Standard Time).

The band covered more than half a square mile and was marching fairly fast, doing more hopping than walking. The situation (fig. 1) was a series of small, low, almost bare stony hills forming one side of a narrow valley running N.N.E.–S.S.W. Between the hills a series of small side valleys, with steep-sided dry gullies in their troughs, ran out to join the main river in which water was still running as a reduced, meandering stream within the main bed. The river bed had steep walls on top of which shrubs were growing luxuriantly.

The majority of the hoppers were spread over the open undulating ground and were marching steadily northwards, thus gradually approaching the river at a slight angle. The exact direction of march varied between due North and 30° East of North from point to point on the open ground, but the variations bore no relations to the slope of the ground. The northward trend continued up, down, or across the slopes, on hill tops or valley floors, in the sun and in the shade, in windy or sheltered positions and unchanged by variations in the direction of the very gentle breeze. On coming to the edge of a vertical-sided gully the hoppers paused, producing an accumulation of hoppers along the brink. Under pressure from those behind, those in front were continually leaping off into space. After " picking itself up " at the bottom, each hopper set off again across the gully in the same direction as it had been marching before, whether or not there were other hoppers in its immediate neighbourhood (fig. 1, A). Most of them started to climb the opposite face of the gully but turned or fell back again to the bottom when it was too steep, only to start climbing again.

In the case under consideration the direction of march was not at right angles to the gully, but obliquely across it from right to left (fig. 1, B). In consequence the hoppers started climbing not vertically, but obliquely, and as the wall steepened, were forced to move more to the left, down the gully. Out of this combination of circumstances developed a new marching direction. Hoppers gave up assaulting the wall after a few failures and marched instead down the gully. Other hoppers, apparently under the influence of the unsuccessful climbers, turned along with them without making any attempt to climb. Once the new movement was established renewed attempts to scale the wall in the old direction became less frequent, the stream down the gully acquiring an " inertia " of its own. In another place (fig. 1, C) where the line of march lay obliquely across a gully from left to right, the new stream of hoppers was deflected up instead of down the gully.

Among the shrubs above the river-bed the individual streams of hoppers were winding in and out along the lanes of bare ground between the plants, often diverted considerably from the direction followed on open ground, but tending always northwards. Only a minority were in or on the plants at a given time.

As the hoppers marched or fell down to the river-bed itself they continued moving northwards until they neared the flowing water. Here, unless there was great pressure of numbers behind, they paused for anything up to a minute. They then began to " potter about " so that there was confusion near the water's edge. Gradually they joined to form streams marching steadily to left and right along the water's edge, for, at the particular point described (fig. 1, D), the water lay perpendicularly across the line of march. Those becoming involved in the westward column were directed round by the turn of the water to a point where they were forced back up the bank in a southerly direction and formed a

dense column which was finally swamped by and incorporated into the northerly drive of the rest of the band. The column moving east came to a point where the water met the bank at an angle of about 45°, and the latter was too steep to climb. Some hoppers began to climb and fell into the water. Most turned right through an angle of about 315° and formed a second southward-moving column also eventually overwhelmed by the northward-moving mass.

Everywhere a few hoppers marched straight on into the water, and where the press was thick many did so after some hesitation. Once in the water they swam vigorously (that is, continued making the same movements as those involved in hopping) in a northward direction, being carried rapidly down-stream in the process. A small number were drowned but the others gained the opposite shore and continued their march northward, although now only in ones and twos.

III. Influence of Separate Factors.

1. *Gregariousness.*

Gregariousness unquestionably plays an important rôle both in keeping the members of a band together and in keeping them moving in the same direction. The mutual mechanical and optical stimulation which produces these effects is plainly seen when hoppers crowd up behind each other in face of an obstacle, jostling those in front until they tackle it, or when moving hoppers overtake stationary ones leading to a renewed advance by those momentarily halted. It is again obvious when a column of hoppers meets another column moving in a different direction and the smaller or looser column gradually assumes the direction of the larger and denser.

The frequent observation that hoppers among thick scrub kept mainly to the lanes of bare ground between the plants even when this involved deviation from the established march direction, was another consequence of the gregarious component in the behaviour. Plants do not constitute an absolute impediment to hoppers comparable to a wall they cannot climb. A number of them did in fact keep straight on until they met and climbed the plants. These, however, immediately ceased to be in close touch with or easily visible to their fellows, whereas hoppers continuing to move along the bare ground, perhaps having turned to do so, remained active and exposed. Thus, the latter and not the former laid down the path that fresh arrivals took. For this reason a plant on which a thin trickle of hoppers climbed and was delayed, was quickly by-passed by a dense stream of hoppers.

The rôle of band density (as a measure of mutual stimulation) was quite the reverse when the obstacle did not separate or conceal the hoppers tackling it, for example a steep bank. Here it was precisely the hoppers that did not turn away or fall off that had the best chance of influencing those pressing on behind. The greater the band density the more unwaveringly were such obstacles surmounted; the less liable was the band to by-pass them.

In the above cases an active and visible minority could determine the general direction of the majority. In the open where all were equally active and visible to one another the majority determined the direction of the whole. It was an everyday observation, and one recorded by other authors, that hoppers starting to move in a direction at variance with that of the surrounding mass of their fellows were soon made to conform with the majority direction. Thus, once a band is well under way any tendency for individuals to take up a new direction in response, say, to a change in an external influence such as the sun

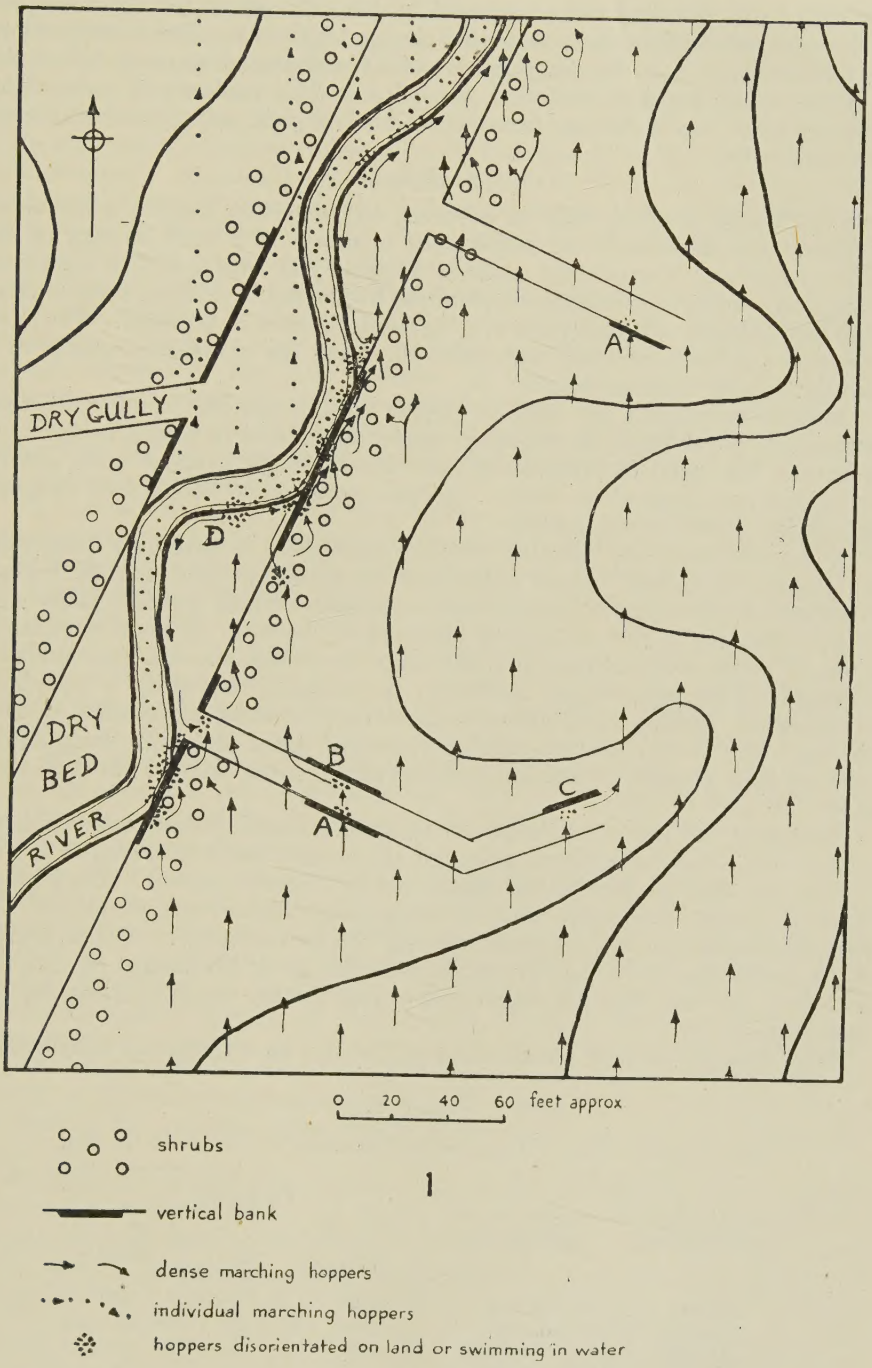

FIG. 1.—Diagram of part of a band marching into a river-bed; Gulumak, Persia, 4th June, 1943. For lettering see text.

(see below), would tend to be swamped by the influence of the other hoppers not at that moment responsive to the changed influence. For in responding to a stimulus such as the sun there is not a simultaneous response by all the hoppers, as experiments confirmed (see below). The tendency of a marching band to resist any deflection from its established path may be termed "gregarious inertia."

2. *Sun.*

Observation showed that in addition to gregarious inertia, some other influence was responsible for keeping the members of a band moving in the same direction. Temporarily isolated hoppers did not lose this direction, even after complete disorientation resulting from a fall. Without some outside directing influence different parts of a big band would have diverged. The most impressive piece of evidence under this head was the parallel movement of a number of quite separate bands.

Parallel movement, not only in varying terrain, but also in quite different landscapes, showed that the directing agency was not to be sought in any local features. The wind was frequently non-existent at the hoppers' level, and its variations were ignored by them. The sun appeared to be the only external agency that could be responsible.

Observers have not recorded whether parallelism in marching disappears on overcast days, but Lépiney (1931) and the present author (in 1937, Sudan, unpublished) have several times observed an effect which provides fairly conclusive evidence of the orientating influence of the sun. A number of small separate bands were all marching the same way when the sun was suddenly obscured. They all stopped marching, the hoppers taking up a disorderly arrangement, making small movements without common orientation as they did so. After a few minutes the sun emerged again and they immediately took up their parallel orientation and moved off in the original direction once more.

Similarly, the lack of consistent marching directions in Kenya was associated with rather cloudy conditions, although the terrain was itself inimical to consistency so that the rôle of the clouds was not thereby proved. The hoppers failed to respond to a mirror (below) during brighter intervals, which indicates that the clouds were in part responsible for the inconsistency. A band marching in a direction at 80° to the sun (Nos. 26–27, Table 1) changed its direction to 20° to the sun after an hour of wavering, halting progress when the sun was clouded over.

The facts in Table 1 are analysed in Table 2 as a frequency distribution,

TABLE 2.

Frequency distribution of marching orientations in relation to the sun.

Angle from due up-sun	Approximate orientation	Frequency		
		a.m.	p.m.	Total
316–45	Towards sun	2	1	3
46–135	Left side to sun	15	6	21
136–225	Away from sun	0	1	1
226–315	Right side to sun	5	4	9
	Totals	22	12	34

and directions perpendicular to the sun predominate conspicuously. In this series of observations the hoppers were keeping the sun on their left sides much more often than on their right. It cannot be said that any common preference was noticed for *basking* with a particular side to the sun, before marching started. Presumably, had similar observations been made on the other side of the mountains, a majority of records with the right side to the sun would have been obtained. As already indicated, the figures in Table 2 do not imply that the hoppers normally reversed their marching direction from south in the morning to north in the afternoon. On the contrary, the impression was that they marched the same way morning and afternoon.

In order to test the hypothesis that marching hoppers were directing themselves with reference to the sun, a mirror was used to alter the sun's position artificially. The trials were made on bands marching in a direction not apparently affected by any local features. It was found necessary to select a point in a band where the hoppers were not dense but formed a thin stream. Otherwise, the few individuals that could be caught in the light reflected by the mirror from the sun were continually impelled forward by new arrivals before they had time to respond.

The procedure was to hold up a blanket so as to shade a section of the hopper stream, while the mirror was held near the ground and in such a position as to throw the sun's reflection on to the shaded area either from the front, side or rear of the advancing hoppers. The people concerned had to keep very still and allow a few minutes for the steady stream to re-assert itself after the disturbance caused in getting into position. Two long series of trials were made on normally marching hoppers. In this condition they continued their straightforward march across the shaded piece of ground. The first series lasted from 0700 to 0930 hours on 5.vi.43. The sun was in the east at an elevation of 35–60° and the hoppers were marching southwards, that is perpendicularly to the sun with their left sides towards it. The mirror-and-blanket technique was tried at several different points in the band and the responses of some hundreds of hoppers observed.

With the mirror opposite to the sun, so that the hoppers had the sun's reflected image on their right instead of their left sides, practically all of them stopped, turned about and marched off in the opposite direction, having thereby brought the " sun " back to their left sides where it had been before they entered the shadow of the blanket. The effect was most striking. It was possible to make a hopper, or even a small group of them, march regularly up and down like soldiers on a parade-ground, simply by removing the blanket and the sun's reflection when the hoppers reached the end of the blanket shadow, so that they reversed and advanced in their original direction again in the light of the real sun, then restoring the shade and the sun's reflection, and so on.

With the mirror held in front of the hoppers the majority of them continued to move forward towards it, but about 10% turned to the right through 90° and marched off, keeping the mirror on their left sides. With the mirror held behind them, the majority again continued without response, but about 30% turned to the left through 90° and moved on with the mirror on their left sides.

The second series of trials lasted from 1500 to 1600 hours on 23.vi.43. The sun was in the west at an elevation of about 45° and the hoppers were marching southwards, that is with their right sides towards it. A large number of hoppers were again tested. With the mirror opposite to the sun the results were as striking as those obtained in the previous series, practically all the hoppers

turning about and marching with their right sides to the mirror, until they emerged into the sunlight again. A larger mirror was used here, about 30 × 45 cm., and as many as 8 hoppers were made to reverse together. With the mirror ahead of them, more responses were obtained than in the first series, about 70% of the hoppers turning left to move at 270° to the mirror, while 30% were unaffected. With the mirror behind the hoppers, only about 10% turned right to move at 270°, the others showing no response.

Three series of trials were made shortly before sunset on 4.vi., 24.vi. and 2.vii.43, when the march was slackening. Those still moving kept to the general direction in which they had been marching, but less accurately, with increasing numbers pausing, dropping out and climbing plants. With the mirror at 180° to the sun some hoppers reacted as before, turning and moving in such a way as to keep the sun's image in the same direction as the sun itself had been. Others turned and moved directly towards the mirror. Others stopped moving and sat broadside-on to the reflected rays of the sun, with or without turning round first. In this way they were repeating what many of the hoppers on plants in the vicinity were doing, sitting on plants broadside-on to the sun itself, regardless of which side was illuminated. Others again were unaffected by the mirror.

Further trials were made on 25.vi.43 in the heat of the day, when the majority of the hoppers were not marching at all, but resting in cooler positions on plants. The first of these trials was made at 1100 hours on some of the active minority in the open, where they were hopping frenziedly along southwards (soil surface temperature over 55° C.; reading of plain unshaded thermometer just off the ground 39° C.; shade temperature at 5 feet, 33° C.). They turned off, climbed and rested on any plant they approached, and stopped marching when they got into any shade (temperature where hoppers were resting 33–34° C.). Where the hoppers were more scattered their southward trend disappeared and was replaced by one directly away from the sun. These hoppers had little forward momentum in the absence of stimulation from their fellows, and moved only a few yards before climbing off the ground. They joined again in the southward trend when the whole band resumed marching later.

As might have been expected, trials at this time with the blanket and mirror were negative. As soon as the hoppers entered the shade of the blanket they stopped marching and " pottered about," showing no response to the mirror. On the contrary, they often turned and made straight for the blanket. This effect was a temporary one, lasting, presumably, only as long as it took for the insects' bodies to cool down to a tolerable temperature, since in the long stretch of intermittent shade under an adjacent avenue of trees marching was resumed in the previous southward direction well before it was resumed in the open.

The interesting point was that the hoppers had been marching southwards all morning with the sun on their left, and were continuing to go south at the time of some further mirror trials (1430 hours), when the sun had shifted into the western sky and was therefore now on their right. Yet, they reacted to the mirror in such a way as to keep the " sun " on their right sides no less consistently than they had kept it on their left sides previously.

The following conclusions may be drawn.

(i) Marching hoppers show a clear " light-compass-reaction," whereby any sudden change in the apparent position of the sun is " compensated " by a turn which restores the sun's image to its previous position in the eye. Normally,

sudden changes in the apparent position of the sun can arise only from a hopper's own deviations from a straight path : the light-compass-reaction serves to correct such deviations.

(ii) The angle of orientation to the sun, although preserved in this way against sudden changes, does not remain constant for a period of hours. It may shift through 180° in the course of a day, for the hoppers continue in one direction while the sun shifts from east to west. Thus, there is no evidence that slow changes in the sun's position produce a re-orientation response : the reaction is subject to adaptation in this respect. The light-compass-reaction serves simply to maintain whatever orientation to the sun has prevailed during the period immediately preceding.

(iii) The compass-reaction is suppressed if opposed by the stimulation of numerous fellow-individuals, that is, by gregarious inertia.

The existence of a light-compass-reaction was to be expected on *a priori* grounds. The sun's apparent diurnal movement from east to west is, of course, a far slower movement than that of other objects in the field of view of marching hoppers. It would be surprising if hoppers did not develop a " fixation " (compensation) reaction to this one relatively constant feature of their visible environment, just as they do to the other, even more constant feature, fellow-hoppers. What was presumably an example of a light-compass-reaction has already been described in the laboratory by Volkonsky (1939), who found that hoppers marched round and round a source of " cold " light.

The light-compass-reaction has long been familiar as a supplementary directing agent in the behaviour of ants and bees (see Wigglesworth, 1939). The directed movement of a " homing " ant or bee involves a complex of reactions, one of which is a compass-reaction to the sun. The compass-reaction can be made to work at variance with the other responses by changing the sun's position suddenly with a mirror, or by shifting the insect away from its normal route. Alternatively, if a " homing " ant or bee is put in a box for some hours and then freed again, its path diverges from the " correct " one. The angle of divergence equals the angle through which the sun has moved while the insect could not see it. For the insect, being shut up in a box while the sun moves and then released is equivalent to the sun's position being changed with a mirror. In both cases the sun moves too quickly for adaptation to occur, so that the reaction produces a deviation instead of fulfilling its normal function of preventing deviations.

3. *Terrain.*

On a large scale there appeared to be some connection between marching direction and ground slope, in as much as there was a general movement from the hills down into the valleys. Volkonsky (1942) reports a similar down-hill trend, as does Predtechensky (1935), but Fraenkel (1930), for example, found an opposite tendency. It seems very doubtful whether such movements involve any reaction to gravity, since in Volkonsky's, Fraenkel's and the present observations hoppers marched up and down slopes indiscriminately, whatever the general trend at the time. It can hardly be supposed that hoppers react geotactically to a slow change of level achieved in the course of a complicated series of ascents and descents. The causes of the general descent from hills to valleys remain unknown. A variety of factors may be concerned, such as the greater windiness of upper levels, or a tendency to move in the lightest, most open direction.

Something has already been said in Part II to illustrate the effects of the

various components of terrain considered on a smaller scale, in their clash with gregarious inertia. Volkonsky (*loc. cit.*) described young marching hoppers as following the direction of greatest steepness, whether upwards or downwards. That statement appears to go too far, but Volkonsky's description of hoppers following the line of " maximum mutual visibility " was entirely confirmed in the present observations, as already outlined. The common remark that hoppers " follow the line of least resistance " is not strictly correct, for that expression lays too much emphasis on the mechanical rôle of obstacles. In fact, a subdivided obstacle like herbage is bypassed because the hoppers that enter it are halted and become hidden, thus ceasing to affect their fellows. A solid obstacle is surmounted without deviation because hoppers tackling it remain in full view even if somewhat slowed. Visual interaction between hoppers is the crucial factor in both cases.

The optical mechanism by which features of terrain produce their directing effects is of particular interest, for it emphasises the overriding importance of optical responses in gregarious locust behaviour. Volkonsky (1942) has brought fresh evidence on this key point by showing that responses to other stimuli yield increasing place to optical ones as hoppers pass from the solitary to the gregarious phase.

It was observed frequently that small streams of hoppers winding along a dry stream-bed, along a lane through low shrubs, or in like situations where the sides were fairly regular, repeatedly turned the corners without touching the sides. Evidently they continued, as they moved along, to keep at an approximately fixed distance from the walls by visual means. The hoppers seemed to be reacting in such a way as to keep their visible environment as constant as was compatible with their own continued movement. This is a type of behaviour somewhat akin to the optical compensation reactions to other hoppers or to the sun, discussed elsewhere.

Optical responses were also involved in the deflection of marching hoppers by running water. In the case mentioned above the hoppers halted near the edge of sparkling water, sometimes within a few centimetres of it and sometimes as much as 30 cm. short of it. The halt was not merely due to a damp sand surface here, for it occurred also on dry sand and stones. Some of the hoppers then made curious, slow, jerky, side-to-side swaying movements of the anterior end of the body, without moving the feet, as if " peering " at the water. These movements did not appear to be a mere shock-effect. There was a brief pause between halting and the start of " peering " movements. The latter were firm and definite and did not suggest any loss of co-ordination or tone but rather the opposite.

Similar behaviour was observed on another occasion in Persia, when hoppers came upon a running irrigation channel after they had surmounted a small ridge which hid the glittering water from them until the last moment. Halting, " peering " and then turning to move along the top of the ridge without going down to touch the water, were here even clearer than before.

" Peering " has been observed very frequently both in the present and in a previous investigation. It was clearly displayed whenever a hopper, solitary or gregarious, experienced a sudden change in its field of view, due either to its own movements or to extraneous ones. Hoppers coming to the top of a wall, for instance, or reaching the brink of a miniature precipice, stopped as soon as the new vista opened before them and " peered " about before taking any further action. Similarly, if an observer makes a sudden but not too violent movement in front of a moving hopper, it often stands " peering " at him for

some seconds before it advances again. " Peering " may be regarded as the most conspicuous, extreme form of the reactions which must occur in less dramatic a manner to produce the tendency to follow the " line of maximum constancy of the visual field " mentioned above.

The anthropomorphic term " peering " is used here for the sake of brevity. Admittedly it is not a literal description but one in terms of a probable effect, that of sharpening vision. Naturally, the swaying movements may have some significance for other senses as well.

Another optical response, attraction to conspicuous shadow-casting features like shrubs and trees, was not noticed except in the heat of the day or the evening; that is, at times when gregarious inertia and the light-compass-reaction are weakened. This attraction has been demonstrated experimentally in the field at other times of the day, but only in isolated, non-migrating hoppers (Bodenheimer, 1944; Kennedy, 1939). In one place where a large band was moving past an avenue of trees at mid-day, the hoppers at a distance moved on but the whole strip of the band within 50 feet of the trees was deflected towards them. A light wind was blowing in the same direction as the latter hoppers, not from the trees to them. The slowing of the hoppers' march by mid-day high temperature lasted several hours at that season in Persia, so that this attraction must have helped materially in drawing bands into villages once they came close. According to Volkonsky (1942) such attraction becomes stronger in dry conditions.

4. *Wind.*

It will be seen from Table 1 that less attention was paid to this factor, owing to a repeated impression that hoppers were not importantly affected by it. Temporal or local variations in wind strength and direction did not noticeably affect hoppers. The few records in the Table suggesting a preference for marching in line with, rather than across the wind, are quite inconclusive. The powerful " dust-devils " that were fairly common in Persia had only a passing disruptive effect and were not big enough to affect the whole of a band at once. Winds were generally light, however.

Light winds would be more likely to affect hoppers before gregarious inertia and the light-compass-reaction had stabilised the march direction, that is at the start of marching. This was not observed, but the possibility arises that parallelism between separate bands was due to their all being influenced by the same general wind when marching began. Unfortunately the point cannot be settled without more observations on local winds at the start of marching by separate bands on the same day.

The case against an important rôle for the wind is, however, strong. It rests on the known weakness of early morning winds, on the certainty that a general wind would acquire a variety of directions and strengths in mountainous country and on the certainty that the wind on the ground where the hoppers are would be weaker and still more variable.

The evidence in the literature on wind and marching directions is conflicting (see Kennedy, 1939). Some authors have reported persistent down-wind movement, but among these Fraenkel (1930) also observed marching due up-wind. When he took hoppers from a band moving down-wind and released them away from their fellows, they marched promptly up-wind. Careful observation of many isolated *solitaria* and *dissocians* individuals on open ground (Kennedy, 1939) established a definite tendency to move up-wind.

On the whole, it appears that when down-wind migration occurs it is a coincidence, the direction being due to other causes, while wind is not, in general, an important directing influence.

IV. Discussion.

The present observations have confirmed that the direction of marching may be influenced profoundly by the terrain, and have brought out the important part played by optical responses as the mechanism of such influence.

Of greater interest are the observations of movement on more or less unobstructed ground, which throw some light on the remarkable constancy of a given band's direction, and perhaps on the phenomenon of parallel movement among separate bands.

It was concluded that parallel movement within a band at any given time and likewise the whole band's continued movement in one direction, were attributable to two mechanisms. The first is gregarious inertia, the direct result of the compensation responses hoppers show to each others' movements. Gregarious inertia is the more powerful, the more densely-packed the hoppers are. The second mechanism is the light-compass-reaction, by which each hopper preserves a certain angle between its body axis and the sun. This angle is not permanently fixed, but is laid down by previous events. As soon as a hopper has been kept at a certain angle to the sun for a period, it begins to resist any sudden change of that angle by making compensatory turning movements. These compensatory responses are suppressed, however, in a crowd of hoppers.

The manner in which these two mechanisms operate in practice follows from the characteristic structure of marching bands. An essential feature of marching bands is their fluidity. In the present study all bands observed on unobstructed ground had indefinite outlines and varied greatly in density from point to point, and from time to time at any one point. Uvarov (1928) and Fraenkel (1932) quote some cases in which bands showed a long, sharply-demarcated " front " along which the hoppers were densely crowded. No hoppers strayed beyond the front, while many straggled out to a ragged rear, providing a most striking demonstration of the optical compensation responses comprising the " gregarious instinct." In both types of band, irregular and " fronted," there is continued overtaking and replacement of one hopper by another. Any given individual spends some time in a dense press of its fellows, then finds itself comparatively isolated, and so on.

It is at once apparent that these are conditions in which gregarious inertia and the light-compass-reaction can play complementary rôles. While it is in a dense crowd of its fellows, a hopper is kept on a straight path by gregarious inertia. The light-compass-reaction cannot appear in such circumstances, but gregarious inertia, by holding the hopper at a certain angle to the sun, serves to fix or " imprint " that angle on the hopper. Now, if the hopper becomes isolated its light-compass-reaction serves to preserve that angle and so keeps the hopper moving in the same direction as its fellows without any direct influence from them. Neither gregarious inertia nor the light-compass-reaction could alone ensure continued migration by whole bands in one direction. Jointly, the two mechanisms do so very effectively.

At first sight it appears impossible for this dual mechanism to carry forward the direction followed in the morning when a mid-day halt intervenes before marching is resumed in the afternoon. It is perfectly possible, nevertheless, for the author has never seen a mid-day halt that involves 100% of the hoppers

simultaneously. Where there was little shade, some of them were always to be seen hopping vigorously along while their fellows were pausing on plants. Where there was enough shade to cool them, marching was resumed by large numbers together. Such movements may never have carried the individuals involved very far, but the fact remains that some movement was always going on. It has been emphasised already that it is the moving and not the settled hoppers that determine direction when the two are mixed, even if the moving ones are a minority. The dual mechanism outlined above can thus preserve a constant direction through an incomplete mid-day halt and on into the afternoon.

There is little quantitative information on the speed of adaptation of the light-compass-reaction. Isolated hoppers were seen to maintain their direction for many minutes, and there was no evidence they could not do so for much longer. This suggests that adaptation is relatively quick, and that the apparent movement of the sun due to the earth's rotation is too slow to evoke any response. By the time the sun's image has moved from one position to another in the eye, the hopper is already " fixing " the sun in the new position, and does not therefore deviate from its previous path. In that case the light-compass-reaction alone might ensure a fixed direction of marching right through the day. This seems especially probable in the tropics where the angular velocity of the sun's diurnal movement in the *horizontal* plane is small, for the hoppers' direction of movement is determined, of course, by its orientation in the horizontal plane. Actual cases of bands marching in the same direction all day (*e.g.*, Lépiney, 1931; Fraenkel, 1930; Kennedy, in this paper) do not settle this question, owing to interference by gregarious inertia.

There are a few recorded cases of hoppers keeping the same angle between themselves and the sun throughout the day. Thus Zimin (1931, 1934) claims that hoppers of *Calliptamus italicus* and *C. turanicus* always moved perpendicularly to the sun with their left sides towards it, so that they marched south in the morning, then south-west, west, north-east and finally north in the evening. Other cases of hoppers following the sun round through the day, but in this case moving towards it, are given by Koeppen for *Locusta migratoria* (1870) and Köhler (1937) for *Schistocerca paranensis*. Here it appears that adaptation of the light-compass-reaction was slow enough for the hoppers to react to the apparent movement of the sun across the sky. The facts are insufficient to judge whether this is due to peculiarities of the species concerned, the season and latitude, the absence of gregarious inertia (scattered migration) or some other cause.

If gregarious inertia and the light-compass-reaction provide an efficient mechanism for preserving a given march direction once it has been established, the question arises as to how that direction can be altered, and how it is established in the first place when marching starts. We have already seen that terrain plays some part in this, diverting bands and sometimes, if in a manner not yet understood, imposing a common direction on separate bands. Apart from terrain, it seems highly probable that the direction taken by a band when it starts to migrate in the morning depends upon the orientation of the hoppers before they move off, during basking. It is well known that hoppers sit perpendicularly to the sun's rays during the morning basking period. We should expect that hoppers held in this way, at a certain angle to the sun, would come to " fix " the sun at that angle and preserve it so when they move off. In fact, the work of Grassé (1922), Fraenkel (1930) and Volkonsky (1939) has shown that an optical fixation reaction is apparent already in resting locusts,

superimposed upon and re-inforcing the primary orientation reaction to radiant heat. If the basking hoppers are orientated perpendicularly to the heat-rays from the sun and have already acquired a light-compass-reaction serving to preserve that orientation, which in some hoppers is 90° and in others 270° to the sun's rays, then, as more and more of the hoppers began to move, gregarious inertia would ensure that the whole band moved off either at 90° or 270° to the sun, not part one way and part the other.

Such a train of events was only observed once in the present study, but it seems reasonable to assume it was customary, since marching orientations perpendicular to the rays of the morning sun were much more often seen during the day than orientation in line with the morning sun (Table 2). To account for the preference for the " left-handed " (46–135°) as against the " right-handed " (226–315°) orientation there is only a partial, suggested explanation in terms of the local terrain and the tendency to move down-hill. This is unsatisfactory, and one hesitates to resort to the explanation Zimin (1931, 1934) advances for his observations, to the effect that the hoppers themselves have a preference for the " left-handed " orientation. Similarly, Lépiney's observations (1930, 1931) of numerous bands moving consistently to the north-north-east despite daily and nightly halts, may be connected with the perpendicular orientation to the sun before the start of marching in the morning, but here again some other explanation of the choice of northward rather than southward movement is required. The north-easterly prevailing wind may account for it.

In other cases the common direction of marching by separate bands was towards the morning sun, not at right angles to it. The bands observed by Fraenkel (1929) continued to move eastwards all day. Those observed by Koeppen (1879) and Köhler (1937) continued to face the sun all day as already described. Koeppen gives no details, but Köhler's brief account implies that the hoppers had turned to sit facing the sun before migration began. Fraenkel does not mention any change to an end-on orientation before migration started, but he does say that marching began when the temperature of an exposed thermometer just above the soil surface exceeded 27° C. In the present studies marching (by young hoppers of *Schistocerca gregaria*, as in Fraenkel's case) began already when a thermometer similarly exposed reached about 20° C. Possibly the different orientations may be explained on this basis. As Volkonsky (1939) and others have shown, locusts change their orientation to radiant heat from one perpendicular to the rays to one facing the heat source when their internal body temperature reaches 36–37° C. (Ist–IIIrd instar *Schistocerca gregaria*). It is probable that Fraenkel's hoppers were already close to that temperature when they began to move, and on moving would have become still warmer. In that case they might have changed their orientation to the sun as they moved off, but before mass migration had set in, with the result that the orientation towards the east, not towards north or south, was the one " fixed " subsequently by gregarious inertia and the light-compass-reaction.

In the present studies the hoppers were apparently cool enough to start marching perpendicularly to the sun's rays, and even if later they became heated to the point where their resting orientation would have been parallel to the rays, this did not alter their marching direction. That can be accounted for by the stabilising effects of gregarious inertia and the light-compass-reaction as outlined above, which remain operative even during an incomplete mid-day halt. During such a halt when fewer hoppers are moving, and even these move only short distances at a time, some weakening of those stabilising influences is to be expected. On one occasion some scattered hoppers of a band were seen

to change their direction from that of the main mass (southwards) to one directly away from the sun. They soon climbed on plants. More crowded hoppers did not deviate, and the direction of the band was maintained towards the south in the afternoon as it had been in the morning. The stabilising influences continued to act partly, no doubt, because the mid-day halt and the seeking of cooler situations by the hoppers prevented their internal body temperature from reaching the level where orientation in line with the sun's rays is the overriding feature of behaviour. Unless high temperature and vegetation scarcity conspire to frustrate such temperature-regulation, a complete halt in the sun with consequent change of marching direction is not to be expected.

It should be noted that when the sun is obscured by clouds, depriving the hoppers of an important stabilising factor for their march direction, confusion results, as observed in Kenya. Close parallelism and cohesion within a band are impaired. Separate bands do not follow a common direction. Obstacles and disturbances deflect hoppers more easily. Such deflections are not corrected, for gregarious inertia, operating alone, serves to maintain only the direction of the moment and has no delayed action over an interval of time like the light-compass-reaction. If the sun emerged from behind clouds when hoppers were not marching, so that a basking period took place when the sun was no longer in the east, then the subsequent march direction would be, presumably, different from what it would have been after a normal early-morning basking period.

V. Summary.

1. A number of observations on marching hopper bands, such as have already been recorded in the literature, have been repeated with close attention to detail and some field experiments.

2. It appears that optical responses of various types play a dominating rôle in the behaviour of migrant hoppers.

3. Among these, compensation-reactions to fellow-hoppers are of first importance, endowing a marching band with a tendency to resist external deflecting influences. This tendency is designated as " gregarious inertia."

4. Supplementing gregarious inertia in enabling a constant common direction to be maintained all day despite temporary interruptions, deviations or isolation of individuals, is a light-compass-reaction to the sun.

5. The important influence of various features of terrain on the route taken is largely visual. In relation to obstacles there is a tendency to follow the line of maximum mutual visibility as between members of a band, and a less important tendency to follow the line of maximum constancy of the visual field.

6. The factors determining the choice of direction when marching starts, and those responsible for separate bands moving in parallel, remain incompletely known. The orientation of hoppers basking in the sun before marching starts is probably among them.

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